

XXIV. *On the Anatomy of Victoria regia.*—Part II.

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IN a contribution to the Philosophical Transactions of this Society, published in 1852 (Part II. p. 289), I gave an account of the internal anatomy of the stem or rhizome of *Victoria regia*. I then stated that I regarded the arrangement of the vascular structures as essentially agreeing with that typical in Monocotyledons, and I directed attention to certain points of less importance, some of which appeared to strengthen the general argument in question, while others were opposed to it. Subsequently I have had an opportunity of studying the anatomy and development of the leaves, roots, and flowers of *Victoria*, and of observing some interesting facts which have not been clearly made out in any of the various memoirs which have appeared on this subject. I have also been led to a reconsideration of the subject of the anatomy of the stem by a criticism which appeared in the 'Flora Indica' (p. 236), the distinguished authors of which, in their advocacy of the opinion that the Order Nymphæaceæ is really Dicotyledonous, question the agreement which I have declared to exist between the structure of the stems of *Victoria* and of Monocotyledons.

In the present paper, which may be regarded as a continuation and completion of the former, I shall first deal with the debated question of the structure of the rhizome, and afterwards give an account of the development of the appendicular organs, including the flower, and of the phenomena presented in the germination of the seed. For the absolute determination of the question whether a stem were organized on the Monocotyledonous or the Dicotyledonous type, it would be requisite first of all to define clearly what conditions we regard as typical in the two classes. This is no easy matter in the present state of our knowledge. The old terms Endogenous and Exogenous growth are founded on no corresponding contrast in the organization of the plants to which they refer. Exogenous growth is a reality, but endogenous growth is a figment of the imagination. The general distinctions between the stems of the two great classes of Angiospermous Flowering Plants depend upon a different mode of arrangement of the fibro-vascular bundles, and, usually, in addition to this, upon a different mode of arrangement of the elementary organs in the fibro-vascular bundles. These are the only essential differences; the formation of annual rings is by no means a constant phenomenon in perennial Dicotyledons. It offers, however, a negative character for the Monocotyledons, since, from the construction and arrangement of their fibro-vascular bundles, they cannot produce annual (or periodical) rings of the same kind as those of the Dicotyledons. The layers formed in such exceptional instances as *Yucca*, *Dracæna*, and analogous stems are totally differ-

ent from those of the layers of Dicotyledons, being formed of entirely new fibro-vascular cords quite independent of those of the inner substance of the stem, while the successive layers of the stems of Dicotyledons are ordinarily horizontal developments from the cambium layers of the pre-existing bundles.

Many Dicotyledonous rhizomes, although perennial, form no distinct annual rings, and it is common to find the older parts of these thinner than the younger; the reverse of what is ordinarily seen in trees of this class. But in those cases even where there are no annual rings, it is almost always possible to distinguish the typical arrangement of the bundles of the yearling shoot in a single circle surrounding the pith, with processes of cellular tissue forming medullary rays, running out between them to the rind or bark. This circular arrangement is seen most distinctly when the stem has the internodes developed, but it is evident even when they are little elongated. The arrangement of the fibro-vascular bundles in a single circle depends upon the fact, that the leaves of Dicotyledons are supplied by a comparatively small number (3—5—7) of fibro-vascular bundles which are developed collaterally, and in their course through the few internodes which they traverse, remain side by side, separated by plates of cellular tissue (medullary rays) which are interrupted at more or less distant intervals by collateral anastomoses of the bundles. The bundles supplying the leaves are formed in the bud, and their earliest vessels constitute the sheath of the central pith; as the leaf is carried out from the *punctum vegetationis*, no new bundles are developed, but the fibro-vascular bundles are increased in diameter by the development of wood-cells and ducts at their peripheral surface, and in most cases at the sides, thus encroaching on the medullary rays.

In Monocotyledons it is usual to find the nascent leaf embracing with its base a much greater segment of the circumference of the growing apex of the stem than in Dicotyledons; often it extends all round, so as to appear like, or actually to form a tube, as we see even in the full-grown state of the Grasses and Sedges. Into this wide base run generally a great number of separate, small, fibro-vascular bundles, as is seen very clearly in broad parallel-veined leaves, such as those of the Flag. And when a petiole is formed, the bundles do not unite collaterally as in the petioles of Dicotyledons, but pass out separately, as they run in the stem. Again, as the leaf is pushed outward in the bud, towards the circumference of the stem, the earlier bundles receive no peripheral additions, but in place of this new and distinct bundles are formed on the outer side of the old ones. Further, the new bundles formed for the succeeding leaves are not placed between these older ones, but are formed within and cross to the outside of them, passing down in the peripheral region; those of the next leaf follow in the same way; and when, as is often the case, the bundles traverse a great number of internodes (20—50), a vast number of them must necessarily appear in a cross section of the inferior part of the stem. These bundles contain no provision for enlargement in subsequent seasons of growth: the delicate elongated cells called by VON MOHL *vasa propria*, and compared by him with the cambium structure of Dicotyledonous bundles, are

necessarily incapable of a development similar to that of the cambium region just referred to, inasmuch as they are closed in all round by the other perfectly-formed elements of the fibro-vascular bundle.

The lower extremities of the bundles of Monocotyledons, moreover, do not anastomose collaterally below in the inner part of the stem, as those of Dicotyledons do; they run more or less obliquely outwards until they reach the region where the central substance of the stem joins the rind, at which point they usually branch and anastomose with their fellows above, below, and around, sometimes forming an intricate fibro-vascular plexus. The cellular tissue in the vicinity of this region, forming the division between the rind and the medullary substance, partakes in some measure of the characters of the cambium region formed by the collective bundles of a Dicotyledonous stem, since it is here that adventitious roots first arise; and here also are produced those peculiar fibrous layers of increase which give so anomalous a character to the stems of *Yucca*, *Dracæna*, &c. But it must be observed that there exists this essential difference, that the cambium layer is the outer, horizontally developed region (or outer side) of the Dicotyledonous bundle, while this pseudo-cambium region of Monocotyledons is connected only with the inferior extremities of the closed fibro-vascular bundles.

Applying these considerations to the structure presented by the stem of *Victoria*, we find unmistakeable resemblance to the typical structure of Monocotyledons in the arrangement of its bundles, and the entire absence of that kind of regularity which produces an annular appearance of the fibro-vascular structure in a cross section; the great number and the isolation of the bundles, and the absence of a central medullary region are especially Monocotyledonous; and the relative position of the bundles in their course is closely in agreement. The chief difference consists in the collection of the bundles together into a kind of cord where they run out from the central region into the petiole—which arises from the comparatively narrow base of the leaf at its origin in the *punctum vegetationis*,—and in the existence of numerous bundles connected with the roots running up and down and around the stem in the region immediately within the rind. The former of these points indicates an agreement with the Dicotyledonous type; the latter departs less from the Monocotyledonous type than from the Dicotyledonous.

The general agreement of structure with that typical in Monocotyledons may be admitted without our assuming that this should largely influence us in determining the systematic position of the plant it occurs in. The general resemblance of the leaves of Monocotyledons with dictyogenous venation to those of Dicotyledons, is an example of strongly marked Monocotyledonous plants exhibiting a resemblance in certain characters to Dicotyledons. The weight attributable to such cases can only be estimated after a careful examination of the various modifications they present, and of collateral circumstances.

At first sight the annular arrangement of the fibro-vascular bundles around a central pith appears a very important systematic character, since it is extremely rare to miss it, even in the most irregularly developed rhizomes of Dicotyledons, where little or no pro-

duction of annual rings takes place. On the other hand, we know of no case of its occurrence in Monocotyledons. But although the 'scattered' arrangement is so rare in Dicotyledonous stems, instances of it do actually occur; and one case recently made known by M. VAUPELL* is especially interesting, as it indicates that we must be very cautious in regarding it as a systematic character. In the rhizomes of the genus *Primula* the fibro-vascular bundles usually stand in a circle around the pith, as in *P. vulgaris*, *sinensis*, and others; but in *P. Auricula* the bundles are scattered generally through the parenchymatous structure without any appearance of a distinction between pith and wood, essentially therefore, although in a more simple form, exhibiting the same aberration as *Victoria*. The existence of this character in certain species only of a clearly-marked genus would be fatal to its use as a systematic character, did we not know that no single character in natural classification can be regarded as absolute†. If, however, its importance be admitted, it becomes necessary to inquire how far it is to be allowed to prevail, and what attending circumstances must be looked to in estimating it.

In the present case, when we pass from the arrangement of the fibro-vascular bundles to the structure of the bundles themselves, a most important qualifying circumstance becomes evident. The horizontal and perpendicular sections given with my former memoir‡, show that the fibro-vascular bundles consist of a central group of spiral vessels surrounded by delicate elongated cells, forming a kind of cambium tissue: there is no wood here, nor anything comparable to the so-called liber-fibres of the bundles of ordinary Monocotyledons. The vascular bundles are reduced to their simplest elements,—a few vessels enclosed by a cambium region. In this state they agree with the rudimentary condition of the Dicotyledonous vascular bundle, which is especially characterized by its peripheral region being composed of cambium, giving it the power of growth; while in the bundles of Monocotyledons the cambium tissue is, as a rule, found in the middle part, with the older woody structure external to it, forming a fixed boundary, precluding further growth.

Considering the rudimentary condition of the vascular bundles of the stem, we should perhaps be rash in drawing any positive conclusion from their structure; yet the evidence, such as it is, derivable from this is in favour of the reference of *Victoria* to Dicotyledons.

A far more decided indication in the same direction is afforded by the plan of arrangement of the vascular structures in the roots. The typical structure of the root of a Monocotyledon is that of a cylinder of parenchymatous tissue containing a central woody axis, which axis, when cut across, exhibits a centre composed of more or less

* Untersuch. über das peripher. Wachsthum d. Gefässbdl. der Dicotyled. Rhizome: Leipsic, 1855.

† The so-called 'anomalous' stems of Nyctaginaceæ, Chenopodiaceæ, Menispermaceæ, &c., present conditions which greatly increase the difficulty of laying down a typical character for the stems of Dicotyledons; but researches at present in progress on these structures do not lead to our regarding them as really intermediate between the Dicotyledonous and Monocotyledonous.

‡ Philosophical Transactions, 1852, Plate XX. figs. 10 and 13.

lignified prosenchymatous cells, surrounded by vessels or ducts, the orifices of which form a kind of ring at the point where the central axis joins the cellular rind. This structure prevails in all the Monocotyledonous roots I have examined*.

In Dicotyledons, on the contrary, the woody substance of the root, like that of the stem, always has the vascular elements in the central region and the woody tissue outside it; in fact the root of a Dicotyledon corresponds essentially with the stem, omitting the central pith and the liber-structure of the bark. In *Victoria* the cross section of a root (Plate XXXI. fig. 53) shows that the centre is occupied by the vascular structure, the large open ends of the vessels appearing scattered in a central cylindrical region, which is bounded externally by a circle of compact, small-celled cellular tissue, which may be compared with the woody portions of the vascular bundles of ordinary Dicotyledons. Perpendicular sections made through the region where the roots pass out from the stem, show that the bundles of vascular tissue destined for the root become collected together into a solid cord before entering it, and they then occupy its axis; while similar sections of the origin of Monocotyledonous roots show that a hollow cylinder of vascular tissue arises from the 'fibrous layer' of the stem and passes out in this cylindric form, its centre being occupied by tissue passing gradually from parenchymatous into prosenchymatous, but directly continuous with the central region of the stem. The structure of the root of *Victoria* is therefore according to the Dicotyledonous type.

The structure and germination of the seeds of Nymphæaceæ have long attracted the notice of systematic botanists, and very different views have been entertained on this subject. *Victoria* has been observed in reference to these matters, especially by TRÉCUL, PLANCHON, and the authors of the 'Flora Indica.' My own observations are, however, at variance in several respects with those of all these observers, more particularly in regard to the phenomena presented in germination.

In the ripe seed we find the embryo, enclosed in its special sac (amnion), lodged in a cavity excavated in the perisperm (Plate XXIX. fig. 19). It is of a depressed conical form, the flat base exhibiting a small 'boss' or blunt elevation in the centre, which is the radicle, and this of course looks towards the surface of the seed. The position of the radicle is visible through the amniotic coat (fig. 20 *a*), but it is not until this is removed that the Dicotyledonous structure of the embryo is clearly seen. We then find the conical embryo (fig. 21) presenting a vertical groove running over the summit and down each side, dividing it into two halves, the two cotyledons; and the groove ends in a kind of notch at each side of the base, next the radicle. Separating the cotyledons in the line of the commissure (fig. 21 *d, e*), we perceive that they are excavated internally, so as to form, when applied together, a somewhat globular or very convex lenticular case, enclosing the plumule. The plumule, placed centrally and directly over the radicular papilla, is a fleshy body, somewhat compressed in the direction parallel to the

* A more particular account of this character is contained in a former paper read in 1847 before the British Association, and published in the 'Annals of Natural History,' Series 2, vol. i. p. 180.

commissure of the cotyledons, and presents in its upper part two irregular lobes, standing opposite to each other and decussating with the cotyledons (*f*). These are described by TRÉCUL as the primordial leaves.

In germination the hard seed-coat is opened by the separation of a little lid or cap at the point opposite the radicle, and from the orifice thus formed emerges the sprouting structures of the young plant. In the accounts generally given, it is stated that the cotyledons remain in the seed, and the radicle and plumule emerge together, the latter elongating into a kind of stalk between the cotyledons and the first leaf. I cannot reconcile this account with the facts which I have met with. The cotyledons certainly remain within the seed-coats, and, as it appeared to me, soon undergo decomposition; but I believe that, in addition to this, the first leaf of the plumule (the larger of the two lobes visible in the embryo (fig. 21 *f*')) previously to germination) also remains within the seed-coats. In the specimen I examined the radicle had elongated but slightly, pushing off the lid or operculum, which remained sticking upon its extremity (figs. 23 *r*, 24 *A*, 25 *r*, *o*); at the side of the radicle emerged a stalk-like process (fig. 25, *t* 1), which at a little distance from the seed exhibited a blunt lateral protuberance (fig. 25 *sl*), and there became bent at right angles; beyond the bend a long stalk-like portion succeeded (*t* 2), at the end of which the regular stem with undeveloped internodes commenced its growth (fig. 22). On extracting the germinating plant from the seed-coats (fig. 24), the stalk-like process coming out at the side of the radicle was found to arise side by side with the radicle from a fleshy mass (fig. 25 *pl*), which appears to be the plumule, and not the cotyledons, as usually described. The radicle is directly continuous with the main body of this fleshy mass, which seems to correspond with the larger lobe of the plumule of the embryo (fig. 21 *f*'). The stalk above referred to (fig. 25, *t* 1) seems to be an internode developed immediately above the first, undeveloped, leaf (fig. 25 *pl*), which remains in the seed, merely becoming larger and more solid in texture. The protuberance at the angular bend (fig. 25 *sl*) is probably the rudimentary second leaf (the smaller lobe seen on the plumule, fig. 21 *f*'), indicating the end of the first internode and the commencement of the second. The first, shorter, internodal portion (fig. 25, *t* 1) is not cylindrical, but flat on one side, and twisted upon its axis, by which means the second internode comes to have an ascending direction; it was about $\frac{1}{8}$ th of an inch long. The second internode (*t* 2) was about 1 inch long. It appears from TRÉCUL's account that an adventitious root is sometimes developed at the node where the bend takes place, but this was not the case in my specimen. I had not an opportunity of observing the earliest stages of development of the true stem, which commences its formation in the summit of the second internode, but the specimen which I examined bore all its leaves, and therefore left no uncertainty as to their conditions. TRÉCUL says the leaves are alternate, but that the first two have no stipules, and the first no adventitious rootlets at its base. According to the account in the 'Flora Indica,' the first two leaves are opposite. In my plant the leaves of the rudimentary stem had assumed the spiral arrangement characteristic of the full-grown rhizome, and even the very first penetrated a stipule, like all the succeeding, but as the earliest leaf is rudimentary in form, so its stipule is a mere scale. TRÉCUL's error arose

from his mistake about the position of the stipule, which does not sheath its own petiole, but is always *axillary* to the leaf, and envelopes the next succeeding leaf. The first leaf is necessarily naked outside.

The petioles of these early leaves already exhibit the peculiar thickened base so highly developed on the full-grown rhizome; and the earlier adventitious roots break out from the interior of these thickened petiole-bases, like the bundles of roots on the adult plant (fig. 22). On the base of the petiole of the first leaf I found two rootlets; the petiole of the second leaf emitted three; those of the third, fourth, and fifth each four rootlets.

The structure and development of the rudimentary stem on which these leaves and rootlets are borne, agree very closely with that of germinating Monocotyledons,—for instance, with that of the Grasses; the vertical section (Plate XXX. fig. 26) shows this, representing the scattered arrangement and crossings of the vascular bundles, and the absence of any pith. The vascular bundles of the rootlets (*rr*) are directly continuous with those of the stem; but, as in the full-grown rhizome, the vessels occupy the absolute centre of the root, according to the Dicotyledonous type, and do not form a ring round a central cellular axis, as in the roots of Monocotyledons.

The mode of germination here described appears somewhat anomalous; but if, as the facts appear to indicate, the general arrangement of the axial organs approximates to the Monocotyledonous rather than the Dicotyledonous type, it is permissible to seek among the germinating seeds of Monocotyledons for parallels, in spite of the presence of two distinct cotyledons here. The point of view I should feel most inclined to take is, that while two cotyledons do actually exist, these become dissolved in germination, the primordial leaf of the embryo assumes the usual characters of the single cotyledon of such Monocotyledonous embryos as those of Palms, its radicle and petiolar portion (*tigelle*) emerging from the orifice in the seed-coats, and giving origin, between the radicle and the base of the first leaf, to an elongated internode upon which the second leaf is seated*. The chief difference would be that in the Palm embryo the bud is enclosed in the interior of the '*tigelle*' of the cotyledon, while in the *Victoria* the bud is naked on the side of the '*tigelle*,' opposite the primordial leaf (or third cotyledon), so that it need not break out from the interior of the elongated '*tigelle*,' as in the Palm.

The spiral arrangement of the leaves of the rhizome, with their bunches of roots at the base of the petioles, was described in my former paper, and attention was at the

* Since the above was written, I have endeavoured in vain to obtain more specimens of germinating seeds of *Victoria*. I have, however, observed in seedlings of a *Nymphaea* the conditions described by TRÉCUL and the authors of the '*Flora Indica*,' namely, the cotyledons, soldered together, remaining in the seed-coats, while the radicle and *tigelle* being pushed out as a simple process, soon formed an 'elbow,' at which point the radicle and adventitious roots came off and the second internode rose up to form the tuft of leaves. My *Victoria* may hence have been abnormally developed. GRISEBACH some years ago (*Annals of Natural History*, i. 6) described the germination of *Limnanthemum* from dried specimens; in that case he supposed one of the cotyledons to remain in the seed and the other to emerge. The appearances presented by his drawings approach very much those exhibited by germinating *Nymphaeaceae*, which is one more argument for those who incline to believe in a relationship between the latter order and the *Menyantheae*.

same time directed to the peculiarity of the position of the flower-stalks forming a spiral series midway between the turns of the spirals of the leaves, with each peduncle removed to one side of the axil of its subtending leaf. An examination of the terminal bud of the rhizome rendered the relations of these parts clear to me. The leaves are arranged according to the formula $\frac{1}{2} \frac{3}{1}$, *i. e.* each succeeding leaf stands $\frac{1}{2} \frac{3}{1}$ parts of the circumference of the stem to one side of its predecessor; hence thirteen turns are made round the stem before a leaf appears immediately over any given one taken as a starting-point, and this leaf is the twenty-second in order of development from that taken as zero. In this arrangement numerous secondary spirals are formed according to the well-known laws of phyllotaxy. The mode of succession of the leaves is illustrated by the figure representing the upper end of the rhizome viewed from above (Plate XXVIII. fig. 4).

In the *punctum vegetationis* the origin of the leaves and peduncles was readily seen with a moderate magnifying power (Plate XXIX. fig. 5; XXX. fig. 27). Each leaf arises as a conical papilla, very soon presenting three lobes, the middle one being the blade of the leaf, and the two lateral the two points of the double axillary stipule (fig. 27 *l*; *s*, *s*, *b*). Very soon the blade of the leaf becomes distinctly bounded below by a constricted portion, and a ridge arises running across its inner surface from one stipule to the other; as the parts increase, this ridge rises up and forms the membranous axillary portion of the double stipule standing inside the petiole. The petiole soon becomes distinguishable, and as it elongates it removes the blade more and more from the axillary stipule. The gradual evolution of the blade of the leaf, with its curious inrolled veneration, was traced, but demands no special attention, except the remark that the general plan of veneration consists of the rolling in of the edges towards the centre; but there is a complication in the details from a wrinkled or 'corrugated' condition of the parenchyma in the areolæ between the anastomosing ribs. In the specimen I examined, which was taken up covered with flower-buds, these latter were found of every size, diminishing to a conical papilla in the *punctum vegetationis* (Plate XXX. fig. 27), but only the very youngest that could be distinguished stood in the axil of its subtending leaf. Where this existed the nascent organs were in absolute contact. As soon as they become at all separated by the expansion of the apex of the stem on which they arise, the flower-bud is carried away from the axil and takes its position, where it permanently remains, in the axil of the right-hand half of the double stipule (Plate XXIX. fig. 5, *f* 1, *f* 2; Plate XXX. fig. 27). This is the real explanation of the apparently anomalous position of the flowers referred to in my former paper.

The stipules deserve some notice, both from their size and their condition. As they enlarge with the development of the growing axis, they do not become defined below by a constricted base, but extend on each side of the petiole and form a sheathing structure, which reaches at first nearly all round the stem (Plate XXVIII. fig. 4), and ultimately about one-half or one-third of its circumference. This broad base is continuous below with a rounded projection of the cortical structure of the stem, and it is opposite these projections that the transverse plates of solid tissue are found that form the frame-

work of the excavated structure of the rind*. As the stipules enlarge, they overlap their neighbours to some extent. The left-hand half of each double stipule lies over the outside of the right-hand half of the one older than itself, and its right-hand half is in turn overlapped by the left-hand half of its successor; as this right-hand half has the flower-bud in its axil, the latter becomes furnished with a double covering, which, as the stipules converge inward above, completely encloses and protects the flower-bud until it is pushed out by the elongation of the peduncle. The general character of the stipules is shown in the drawings. Each apparently axillary stipule is distinctly double, and the two halves are, when mature, connected by a membranous plate running across the axil, which base is quite unconnected with the base of the petiole (Plate XXVIII. fig. 3). Each half of the compound stipule has a very distinct midrib, which forms an angular projection in the earlier, more folded state of the organ. It was stated in the former paper that the spiral-fibrous structure soon disappears in the ducts and vessels of the leaf-stalks. This is not the case in the stipules, which exhibit perfect vessels when fully developed.

To this paper are appended some illustrations of the elementary structure of the petioles and of the arrangement of the tissues, which do not require further notice here (Plate XXXII. figs. 59–61).

The external aspect of the stem is rendered somewhat peculiar by the mode of arrangement of the roots, which arise in dense tufts or bundles at the bases of the petioles. The manner in which they emerge from the stem is highly curious, and unlike any other case with which I am acquainted.

The roots are adventitious, and arise in the peripheral part of the central substance of the stem, just below where the fibro-vascular bundles run out to the petioles. No trace of the roots is visible externally until the leaves, especially the petioles, have acquired considerable dimensions (Plate XXVIII. fig. 4); then it is observed that the cortical substance of the stem is protruded so as to form a kind of knob at the base of the leaf-stalk; or perhaps it may be best described by comparing it with a highly-protruding *pulvinus* under the point of origin of the leaf-stalk (Plate XXIX. fig. 8). Ultimately a vertical fissure is perceived in the protuberance, the sides of which gradually separate, with rounded edges like lips, leaving an elongated elliptical slit, at the bottom of which are seen the points of the nascent roots (figs. 11, 12). The roots, densely crowded, make their way out, the oldest at the lowest part, and they are given out in such rapid succession that they form a close bunch. As they emerge and expand, they convert the vertical slit into a large rounded bordered orifice (figs. 15, 16). During the subsequent growth of the roots, the protuberance keeps firm and forms a large projecting knob; but their mutual pressure gives the bases of the roots an angular form, so that when they become detached on the decaying parts of the stem, their ends form the six-sided areolæ shown in the illustration of my former paper.

It has been noticed above that even the earliest roots, the bundles of which consist

* Philosophical Transactions, 1852, Plate XIX. *ff*.

of only two to four rootlets, break out in the same way from the bases of the petioles of the germinating plant (Plate XXIX. fig. 22).

Unlike the petioles, the roots retain the proper character of their vascular structures, and in these, as above noticed, they afford a further evidence of the systematic position of the plant. In the fibro-vascular cord running up the centre of the roots, the spiral vessels are collected in the centre of the bundle, as in Dicotyledons (Plate XXIX. fig. 17, Plate XXXI. fig. 53), whereas in Monocotyledons they stand at the circumference of the bundles. The arrangement of air-chambers, so remarkable in all parts of *Victoria*, is especially elegant in the roots (Plates XXXI. & XXXII. figs. 51–55).

The development of the flower was traced from the earliest period at which the organs could be distinguished. In the youngest bud (Plate XXX. fig. 27), about $\frac{1}{50}$ th of an inch in diameter, the peduncle was surrounded by a circle of nascent foliar organs, which did not then cover in the growing apex. Seen from above, this circle was found to consist of five organs (fig. 28), that is, of the four sepals and the first petal. They stood distinctly in a spiral order (fig. 29), in the succession as regards age indicated in the figure. Within these were a few rounded papillæ continuing the spiral, but soon lost in the rounded *punctum vegetationis* of the bud. This bud showed clearly that the primary arrangement of the organs here is a spiral, and that this spiral is continued from the imbricated calyx into the corolla, where the arrangement is on a complex phyllotactic type.

In the next bud (fig. 30), the four sepals had grown up so as to enclose the younger organs, and they now occupied the whole circumference of the receptacle. In the inside of them appeared nascent petals, and at this time the whole centre was occupied by minute papillæform rudiments of organs. Fig. 31 shows the succeeding stages; and when we come to fig. 32, the centre of the receptacle appears naked,—the first step toward the production of the peculiar structure on which the floral envelopes and stamens are ultimately elevated.

When the bud is about $\frac{1}{10}$ th of an inch in diameter (fig. 33), the centre of the receptacle exhibits a dome-shaped smooth surface bounded by a raised rim, on which are supported the stamens and petals, bounded externally by the calyx. In the next bud (fig. 34) the centre of the receptacle had risen up in a conical form, and the internal surface of the annular ridge was marked by fine grooves, indicating the formation of the free edges of the carpels.

It is unnecessary to describe at length the details of the successively older buds, as their important difference is clearly shown in the drawings accompanying this paper (Plates XXX. & XXXI. figs. 34–50). It will be sufficient to notice two or three points.

The carpels are never completely free from the receptacle, except at the edges which form the stigmatic lines, which lines are carried up on the internal surface of the ring surrounding the ovary, to the 'horns' which stand inside the stamens. The 'horns' appear to consist of the points of the carpellary leaves. As regards the cavities of the ovary, they at first point somewhat obliquely upwards, but gradually, by the develop-

ment of the centre of the receptacle into the columella, they become horizontal, and the horizontal stigmatic lines must be regarded as the ventral sutures of the carpels. The upper portion of the carpels, adherent to the annularly raised part of the receptacle, is developed in a remarkable manner. The central columella is originally conical, but it soon exhibits a constricted base, tapering downward in a reversed conical form. The inner surface of the ring, as it were, moulds itself in this, and sends in a ridge-like process, which fits into the hollow at the constricted base of the columella. Afterwards, as the receptacle expands, this ridge, pointing downwards, is drawn away from its original position, but still continues to grow; the stigmatic lines are seen first running horizontally out over the cells of the ovary, next turning inwards, then curving round the ridge upwards, until ultimately they are lost at the base of the circle of 'horns' bordering the annularly raised receptacle.

From the foregoing account it is evident that the inferior position of the ovary of *Victoria* is only apparent, and that the structure consists of a circle of numerous distinct carpels collaterally united and imbedded in an enlarged receptacle which runs up in a circle around them, carrying up the stamens and floral envelopes, and likewise rising into a columella in the centre, where its expansion carries up to some extent the bases of the carpels and brings them into an oblique and almost horizontal position. This removes any difficulty which might arise in considering the relation of this genus with others where the ovary is distinctly superior.

Many other particulars of less consequence were observed, which for the most part have been correctly explained by preceding observers; such are the structure of the orifices found in the leaves, called by PLANCHON 'stomatodes,' the form of the pollen, &c. For an account of these we refer to M. TRÉCUL's memoir*.

In conclusion, I must briefly allude to the bearing of the facts contained in the present paper upon the systematic position of the Nymphæaceæ. Notwithstanding that the anatomical character of the roots adds one more Dicotyledonous feature to the character of these plants, I am more inclined than ever to regard the structure of the rhizome as conforming to the general type of the stem of Monocotyledons rather than to that of Dicotyledons, among which I have found nothing at all like it. But I do not consider that this character alone can decide the position of the Order, the majority of whose characters are, on the contrary, clearly Dicotyledonous; it merely brings it into the position of a link between the two classes, which are by no means so markedly separated from each other as is often supposed from the mode of their arrangement in Systematic works. A further attempt at the settlement of the true affinities of this Order does not come within the scope of the present paper.

January 1859.

* Ann. des Sc. Nat. sér. 3. Botanique, vol. i. p. 145.

EXPLANATION OF THE PLATES.

PLATE XXVIII.

- Fig. 1. Side view (reduced) of the rhizome of *Victoria regia*, with the older leaves and flowers cut off. This drawing shows the bundles of roots coming out from the bases of the petioles, and the young leaves emerging from the large sheathing stipules.
- Fig. 2. Portion from the centre of fig. 1, showing that the growing point is covered up by the large sheathing stipules: the stipule *s* is axillary, and belongs to the leaf of which *p* is the petiole; *f* is the base of a flower-stalk axillary to the leaf of which *p''* is the petiole, and whose stipule is removed.
- Fig. 3. A sketch showing the axillary position of the stipule and its double nature, having a rib or keel on each side of the petiole.
- Fig. 4. View of the summit of the rhizome, with the leaves, stipules and peduncles cut off close to their origin; showing the arrangement of the organs, the mode in which the stipules ensheath the succeeding parts, and the gradual evolution of the bundles of roots from the bases of the petioles.

PLATE XXIX.

- Fig. 5. Magnified view of the *punctum vegetationis* of the rhizome:—*f*¹, *f*², flower-buds, shifted into the axil of the right-hand half of the stipules; *s*¹ *s*¹, the base of the sheathing stipule of an outer (removed) leaf; *s*² *s*², the base of another removed leaf; *s*³ *s*³, the stipulary portions, and *l*, the blade of the next leaf, within which are several other still more rudimentary leaves,—the central one still a simple papilla.
- Fig. 6. A young leaf, magnified (*ns*, of the natural size).
- Fig. 7. Another, more advanced, also magnified.
- Fig. 8. A more advanced leaf, with its axillary two-keeled stipule and swollen base.
- Fig. 9. Side view of a similar leaf and stipule.
- Fig. 10. Terminal bud enveloped in stipules, with all the leaves older than fig. 8 removed; showing the relative degree of development of the peduncle and flower-bud *f*.
- Fig. 11. Base of a petiole about the same age as in fig. 9, with the early appearance of the fissure whence the roots emerge; the petiole at this time $\frac{1}{6}$ th of an inch in diameter.
- Fig. 12. More advanced stage; petiole now half an inch in diameter, and the blade of the leaf 2 inches long.
- Fig. 13. Side view of a more advanced stage.

- Fig. 14. Side view of the blade of the leaf in fig. 8.
- Fig. 15. Base of a petiole and bunch of young roots, natural size, side view.
- Fig. 16. The same, seen from above.
- Fig. 17. Perpendicular section through the base of a petiole, as in fig. 15; showing the course of the vascular bundles of the leaves (*vl*) and those of the roots (*vr*).
- Fig. 18. A seed, natural size.
- Fig. 19. Vertical section of a seed, showing the embryo (*e*) lodged in an excavation of the perisperm.
- Fig. 20. Embryo (magnified) removed from the seed, but still enclosed in its amniotic sac:—*a*, from below; *b*, side view; *c*, vertical section, showing the amniotic coat and the cotyledons, with the plumule in the middle. The figure *ns* indicates the natural size of *a*.
- Fig. 21. Embryo (magnified) with the amniotic coat removed, showing the distinctly Dicotyledonous structure:—*a*, side view; *b*, from above; *c*, from below, with the central boss-like radicle; *d*, cotyledons separated to show the plumule; *e*, one cotyledon only turned down; *f*, plumule laid bare in side view.
- Fig. 22. Germinating plant, with the petioles, of the leaves 3, 4, 5, 6: 2 is the scar of the removed second leaf, with a minute scale-like axillary stipule remaining; the remains of the first leaf would appear on the other side of the stem.
- Fig. 23. The seed, with the base of the germinating plant emerging from it:—*r*, radicle; *t*, stem (*tigelle*); nat. size.
- Fig. 24. Front (A) and back (B) view of the base of the germinating plant, magnified:—*pl*, the portion contained within the coats of the seed in fig. 23, and apparently corresponding to *f* in fig. 21.
- Fig. 25. Another and more enlarged view of the same structure:—*r*, radicle; *o*, operculum; *pl*, primordial leaf; *t* 1, first internode; *sl*, second (rudimentary) leaf; *t* 2, second internode.

PLATE XXX.

- Fig. 26. Perpendicular section of the young stem represented by fig. 22; showing the pseudo-Monocotyledonous arrangement of the vascular bundles, except in the rootlets *rr*, where they occupy the absolute axis.
- Fig. 27. *Punctum vegetationis* of the rhizome, highly magnified:—*l*, a rudimentary leaf turned back, showing the relative development of the blade *b*, and the stipulary portions *s*, *s*,—the petiole not yet developed; *f*, rudimentary flower-bud.
- Fig. 28. The flower-bud *f* in fig. 27.
- Fig. 29. Diagram of the arrangement of the four sepals and first petal, showing it to be a continuous spiral.
- Fig. 30. Magnified perpendicular section of a flower-bud rather older. In this and the following figure the sketches marked *ns* indicate the natural size.

Fig. 31. A somewhat more advanced flower-bud:—*a*, seen from above, with the sepals turned back; *b*, perpendicular section; *c*, perpendicular section of one rather older.

Figs. 32–35. Successively more advanced stages.

Fig. 36. Perpendicular section, as in fig. 35, with the columella cut out to show the carpels.

Fig. 37. Perpendicular section of the elevated receptacle in fig. 36.

Fig. 38. Horizontal section of fig. 37 at \times , showing the carpels open internally.

Fig. 39. An older bud.

Fig. 40. Cross section of its ovarian portion, showing the carpellary cells closed.

Figs. 41–43. Successive stages.

PLATE XXXI.

Figs. 44, 45. Successive stages; 45 *b*, cross section.

Fig. 46. Magnified fragment of *b* in fig. 45.

Fig. 47. Perpendicular section of a fully-developed flower-bud, showing only one-half.

Fig. 48. Magnified horizontal section of fig. 47, at *a*.

Fig. 49. Section at *b*.

Fig. 50. Section at *c*.

Fig. 51. Cross section of a young root.

Fig. 52. Magnified view of a portion of ditto.

Fig. 53. Centre of ditto, more magnified.

PLATE XXXII.

Fig. 54. Spongy cortical parenchyma, as in figs. 52 and 53, magnified 50 diameters.

Fig. 55. Perpendicular view of one of the septa in fig. 54, magnified 50 diameters.

Fig. 56. Perpendicular section of the origin of a root:—*vb*, central vascular cord; *l*, large lacunæ.

Fig. 57. Portion of a vascular bundle, near the origin of a root-bundle: magnified 200 diameters.

Fig. 58. Perpendicular section of *l* in fig. 56, showing that the lacunæ of the roots do not communicate with the air-cavities in the stem, and that the walls are thickened by a sort of cuticle: magnified 100 diameters.

Fig. 59. Cross section of a petiole.

Fig. 60. The same, magnified: the white spaces are air-canals; the shaded spaces fibrous bundles, composed of dense cellular tissue.

Fig. 61. Highly magnified fragment enclosed in the square space *a* of fig. 60.

Fig. 62. Cross section of a flower-stalk.

Fig. 63. The same, magnified.

Fig. 1. $\frac{1}{3}$



Fig. 2.

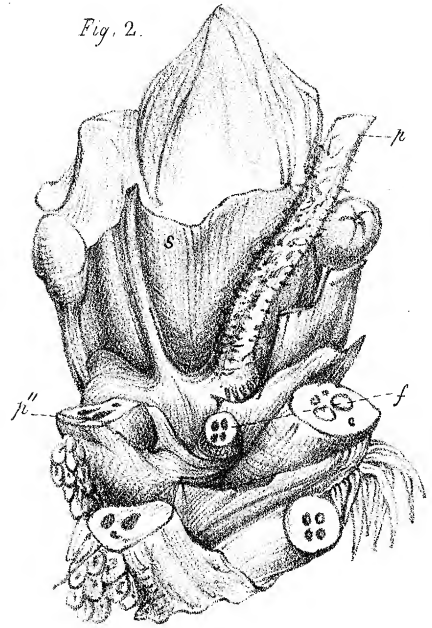


Fig. 3.

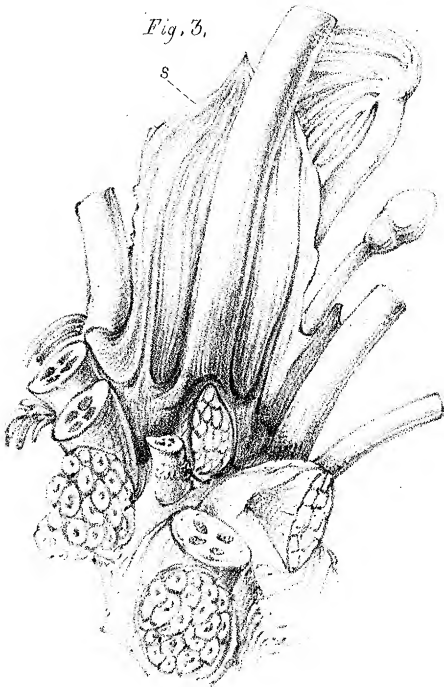
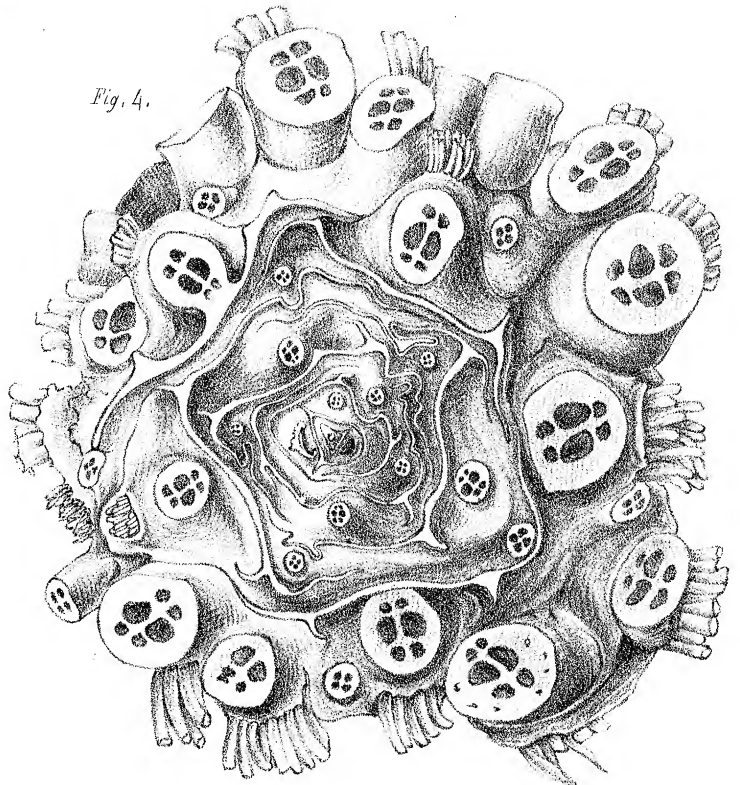
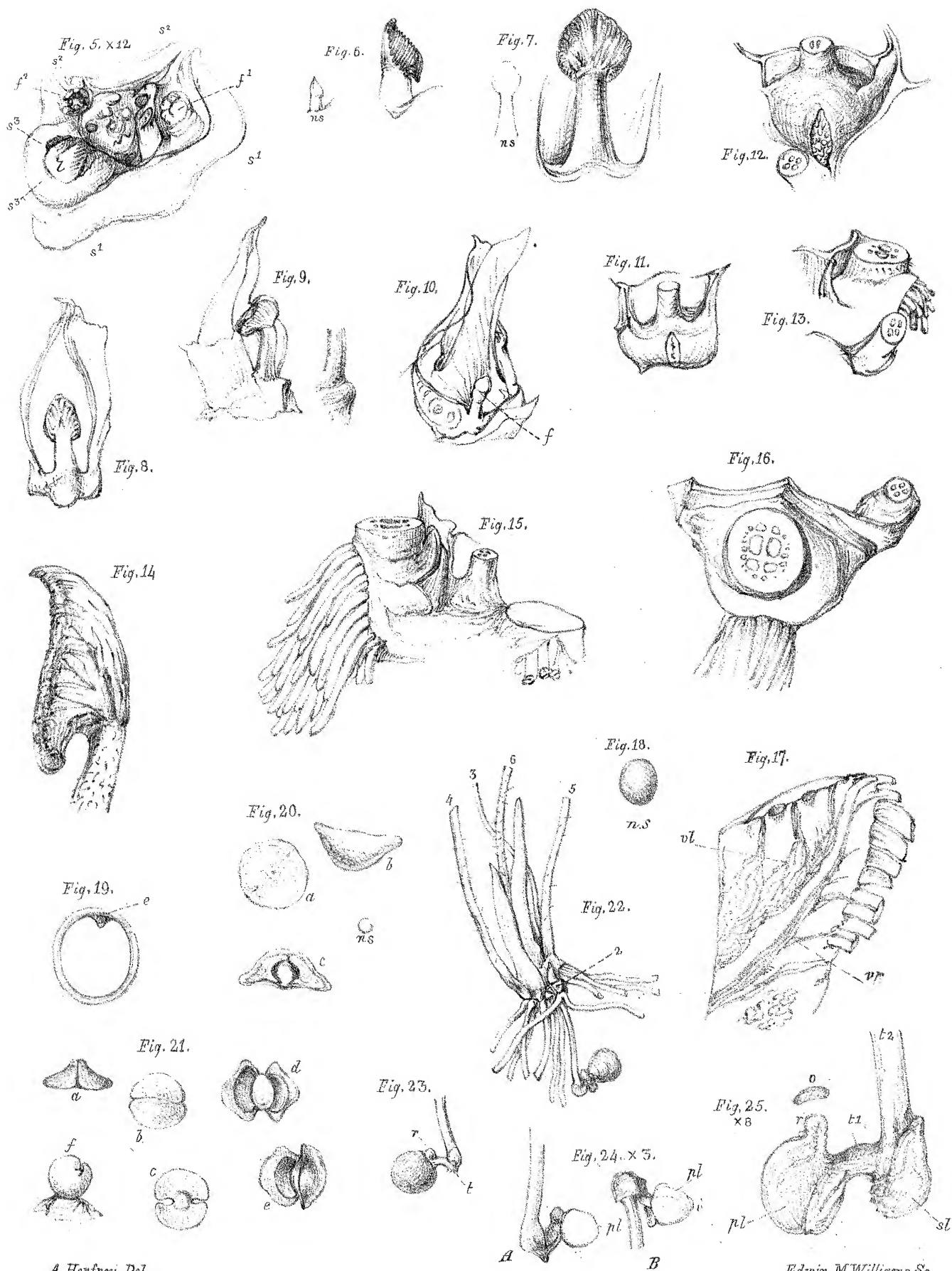


Fig. 4.





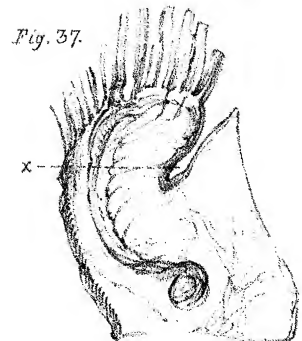
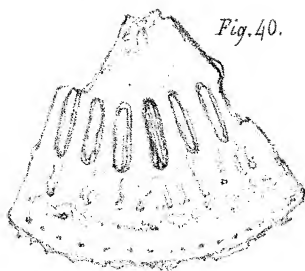
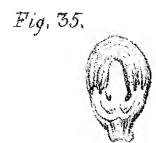
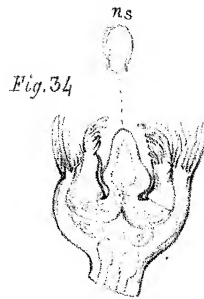
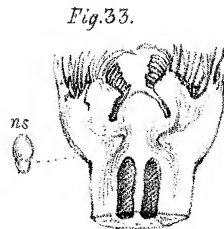
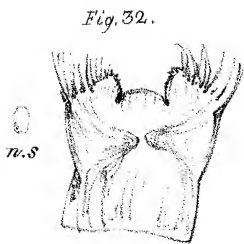
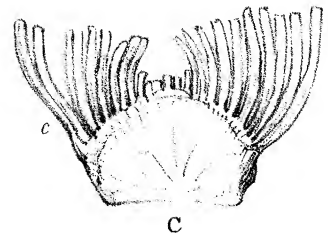
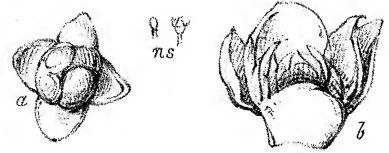
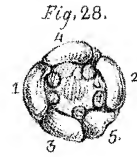
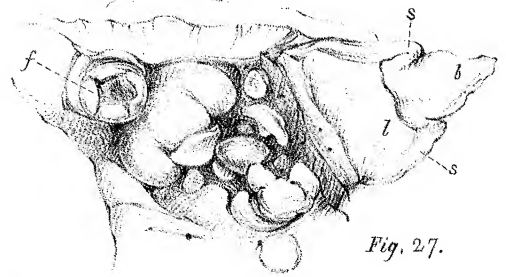
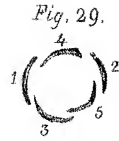
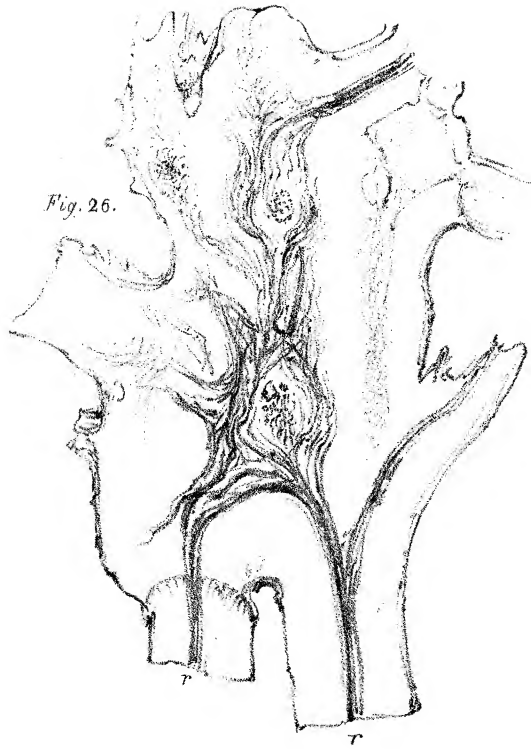


Fig. 44.

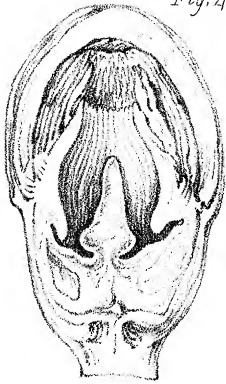


Fig. 46,
 $\times 3$

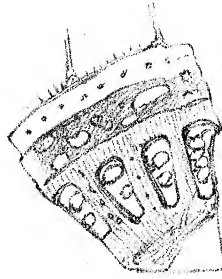


Fig. 45.

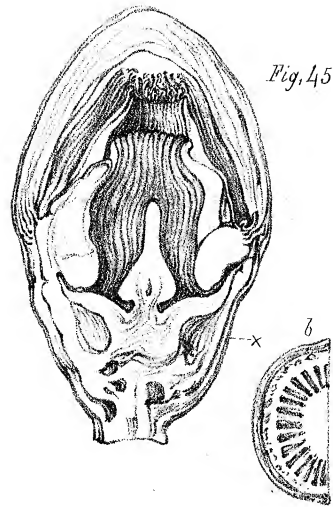


Fig. 49.
 $\times 4$

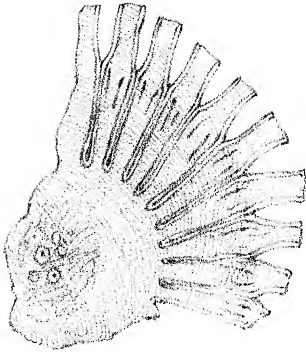


Fig. 47.

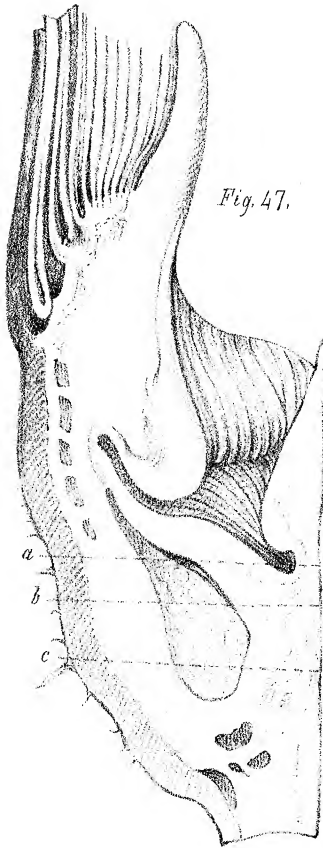


Fig. 48,
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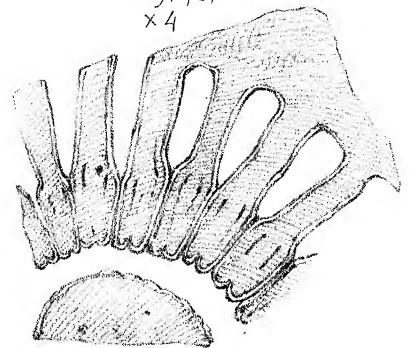


Fig. 52.
 $\times 10$

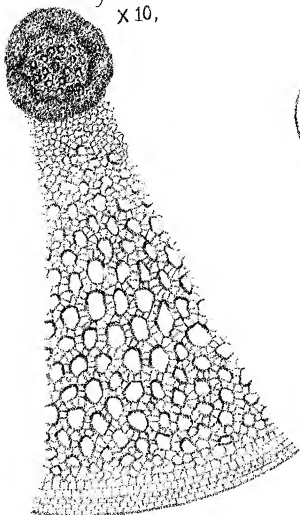


Fig. 51.



Fig. 50.
 $\times 4$

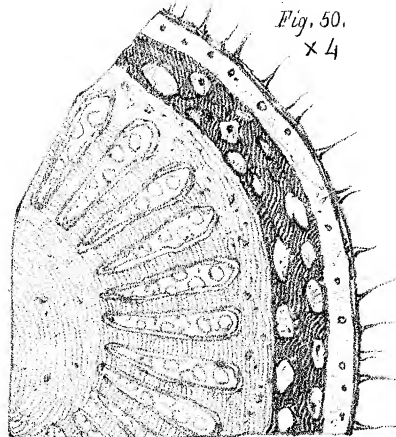


Fig. 53. $\times 20$,

